The Structure and Reproduction of *Gulsonia annulata* Harvey (Rhodophyta)

Elise M. Wollaston[1] and H. B. S. Womersley[1]

Gulsonia Harvey is a little-known mono-typic genus of red algae which has been variously placed in the Cryptonemiaceae (Harvey, 1855, 1860), close to *Crouania* (J. G. Agardh, 1876; Schmitz, 1889) and to *Wrangelia* (J. G. Agardh, 1894, 1897), and in the Nemionales near *Batrachospermum* (Schmitz and Hauptfleisch, 1897; Fritsch, 1945).

Gulsonia annulata was originally described by Harvey (1855) from Phillip Island, Western Port, Victoria and later (Harvey, 1860) recorded from Georgetown, Tasmania. Harvey's collections were apparently sterile, but later J. G. Agardh (1894, 1897), and Schmitz and Hauptfleisch (1897) described carpospores, tetraspores, and monospores without indicating the source of their material. Only in recent years has the alga again been recorded (Womersley, 1948, 1950).

During February, 1956, abundant drift material was collected at Pennington Bay, Kangaroo Island, by the authors. Some 90 specimens were collected as they were washed in over the reef, comprising 51 tetrasporic, 24 female and cystocarpic, 3 male, and 12 sterile plants.

Gulsonia annulata is also known from Sturt Bay on Yorke Peninsula and from Eucla, near the South Australian—Western Australian border. Apparently it is comparatively rare, only being found in drift material from well below low tide level; the plants decompose fairly rapidly when cast ashore.

The following account is based on the rich Kangaroo Island collection of February, 1956.

Shortly before this paper was submitted for publication, Kylin's (1956) account of the Rhodophyta became available. Here Kylin also recognises the identity of *Gulsonia* Harvey and *Crouaniopsis* J. and G. Feldmann, and transfers *C. annulata* (Berthold) J. and G. Feldmann to *Gulsonia* as *G. mediterranea* Kylin nom. nov. The same epithet had also been adopted for the Mediterranean species by the present authors. Kylin, however, gives little more than a formal generic description of *Gulsonia*, and his comments are apparently entirely based on the Mediterranean species.

VEGETATIVE FEATURES

The plants ranged up to 30 cm. in height with an average of 18 cm., and a main axis diameter of 2 mm. The thallus axis and branches are terete, uniaxial, and articulate, with each axial cell bearing from its upper end a whorl of four short branches of limited growth. These whorled lateral branches form nodal bands, less distinct in the youngest parts, where they almost completely cover the axis, and most prominent over the rest of the plant, except in the oldest parts of the main axis and branches where they become obscured (Fig. 1). This is due to the development of 1–3 descending corticating filaments from the basal cell of each short branch, which cover the axis and in the oldest parts of the plant form a dense, tough, and feltlike covering over the whorled laterals as well as the axis. The corticating filaments are simple or sparingly branched, of 7–10 elongate cells averaging 250–300 μ long, by 25–30 μ broad. The axial cells of the thallus are approximately twice as long as wide, reaching dimensions of 1300 μ by 700 μ at the base of the plant. The intercellular connection between cells shows a prominent, thickened platelike structure (Fig. 2c, d).

[1] Department of Botany, University of Adelaide, South Australia. Manuscript received June 4, 1957.

FIG. 1. *Gulsonia annulata* Harvey. Habit of plant showing nodal formation except at base and tips of branches.

The lateral whorled branches consist of 5-7 orders of cells. Cells of the second order are formed dichotomously on the basal cell, thence each cell of successive orders produces a whorl of three cells except the outermost which are borne either in two's or three's. Occasionally the normal terminal cells are transversely divided (Fig. 2b). Cells of each order are progressively smaller, the terminal ones averaging 20 μ long by 6 μ broad. Hairs about 300 μ long, with a swollen tip, are frequently formed from the terminal cells (Fig. 2b). Reproductive organs, young vegetative branches and gland cells are borne on the lateral branch whorls.

Branching of the thallus is irregular, and young vegetative branches may occur on any, except the oldest, parts of the plant. Fach
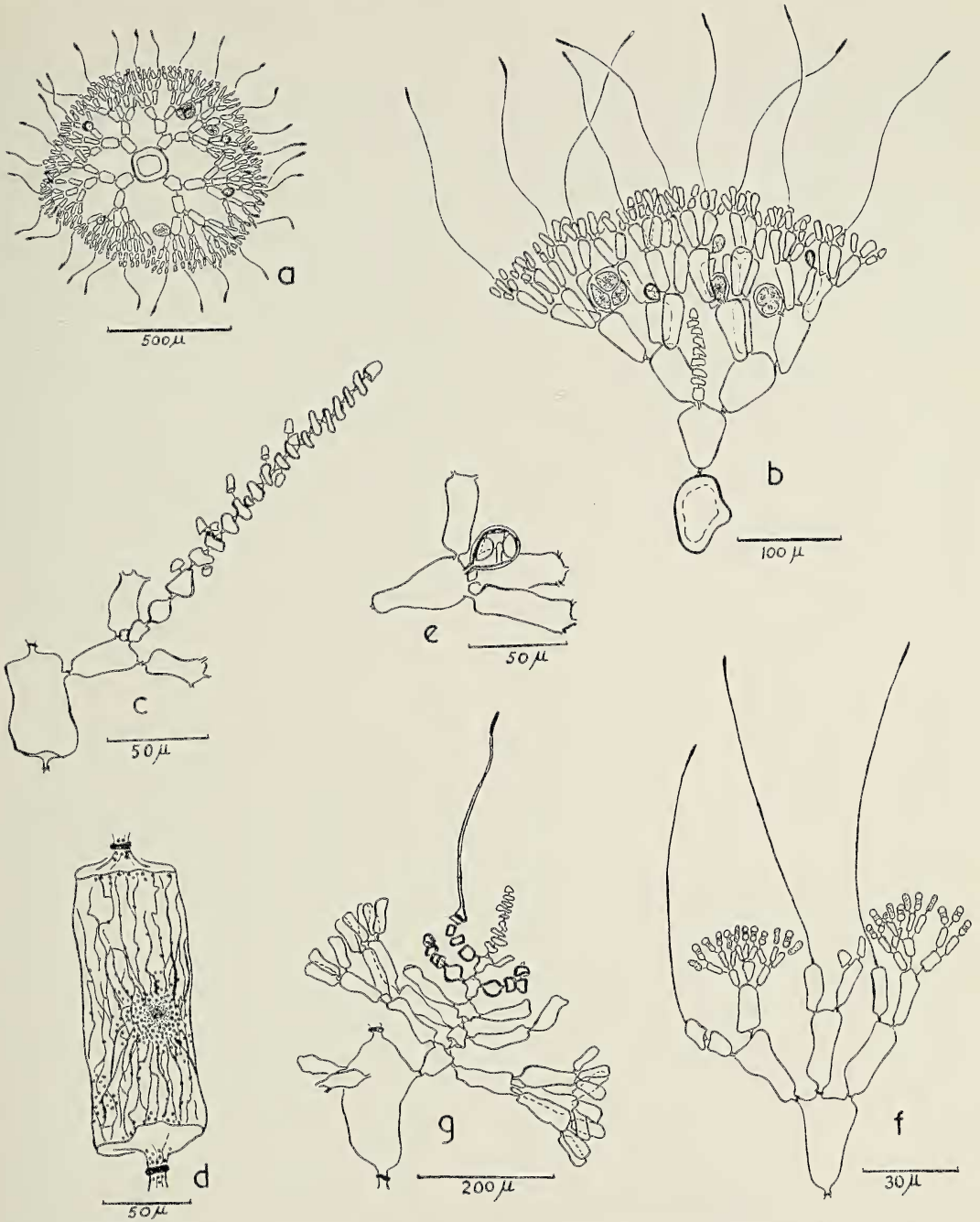
FIG. 2. a, Transverse section of thallus of tetrasporic plant of *Gulsonia annulata* Harvey showing whorl of four lateral short branches arising from axial cell; b, short lateral branch of *Gulsonia annulata* Harvey showing branching by two from basal cell and by three from each subsequent cell, young lateral branch, stages in development of tetraspores, scattered "gland" cells and terminal hairs from some cells; c, development of first lateral cells in young vegetative branch of *Gulsonia annulata* Harvey; d, mature axial cell of *Gulsonia annulata* Harvey showing chromatophore pattern, nucleus, and small granular inclusions; e, "gland" cell of *Gulsonia annulata* Harvey with inclusions; f, terminal spermatangia of *Gulsonia annulata* Harvey with median nucleus; g, fertile branch of *Gulsonia annulata* Harvey borne on basal cell of short lateral branch and bearing two carpogonial branches on the third axial cell and one on the fourth.

branch develops from the outer end of the basal cell of a lateral whorl member (Fig. 2b, c). The initial of the new branch divides transversely, forming a chain of 16–20 cells before cells in the central part of this chain divide laterally to cut off basal cells of the new whorl (Fig. 2c). These basal cells are arranged roughly in an anticlinal spiral, and divide rapidly to form the whorled laterals when the new branch emerges from within the old branch.

All cells are uninucleate, with a large, dense nucleus usually in the mid-part of the cell near the periphery. The chromatophores vary greatly in form, but are constant in any one type of cell. In the outer cells of the whorled laterals they are irregularly platelike, covering almost the whole periphery of the cell. As the cells increase in size the chromatophores change through an irregular anastomosing stage to branched, linear shapes in the larger cells of the main axes. These linear chromatophores tend to converge towards the nucleus (Fig. 2d). Carpospores and tetraspores contain chromatophores which form an irregular, granular network. The nodal or banded appearance of the thallus is accentuated by the denser chromatophores in the small outer cells of the whorled laterals, giving a deeper colour to the nodal bands. In older axial cells, covered by corticating filaments, the chromatophores are greatly reduced. Most cells contain numerous cytoplasmic granules, often concentrated around the nucleus, and at the cell junctions (Fig. 2d).

Pyriform "gland" cells, with a thick mucilaginous wall, occur on cells of the whorled laterals (Fig. 2b, e) in all plants. These cells average about 30 μ in length and each contains several larger inclusions of varying but definite form (Fig. 2e). These may be the "monospores" referred to by Schmitz and Hauptfleisch (1897), but are probably comparable to the gland cells of other genera of Ceramiaceae.

The whole thallus is enveloped in a mucilaginous matrix, making it quite slimy.

TETRASPORANGIA

Tetrasporangia are produced in the upper parts of the thallus, on the outer end of cells of the third order of the whorled laterals. Only one tetrasporangium develops on a single cell (Fig. 2a, b). The sporangium is at first spherical, uninucleate, and sessile, attached by a thin cytoplasmic connection. It reaches 70–80 μ in diameter before division commences. The nucleus divides twice, and with four nuclei present the protoplast division commences at the periphery and proceeds inwards, giving four uninucleate tetrahedrally arranged spores (Fig. 2b). Meiotic figures were not seen in the material available. Accumulation of Floridean starch is indicated by red staining with iodine in tetrasporangia over about 50 μ in diameter, the staining becoming deeper in mature spores. Mature tetrasporangia are about 80–90 μ in diameter.

SPERMATANGIA

Male plants bearing spermatangia are not easily distinguished from sterile plants, but are slightly paler in colour and "rougher" in appearance. This is due to the spermatangia which are formed from the majority of the terminal cells of the whorled laterals. Each normal terminal cell bears a further two or three whorls of small cells, the outermost being the spermatangia. These spermatangia are 8–9 μ long, constricted in the centre, with a median nucleus and two prominent vacuoles (Fig. 2f). Spermatangia are not formed from the occasional terminal cells which divide transversely. Spermatangia are 3.5–4 μ in diameter.

FEMALE PLANT AND CARPOSPOROPHYTE

In female plants, special branches, initially similar to young vegetative branches, occur at short intervals along the axis of main branches. However, normal vegetative growth ceases with the development of carpogonial branches, which are produced either singly or in opposite pairs. Most commonly the third

or fourth axial cell (from the base) of the fertile branch bears two carpogonial branches, while the cell above it (fourth or fifth) bears one (Fig. 2g). Carpogonial branches have, however, been found on axial cells up to the seventh, and occasionally four or five on one fertile branch. Only one carpogonial branch on each fertile branch ultimately gives rise to a mature carposporophyte; in fact, not more than one mature carpogonial branch with a trichogyne was ever observed on a single fertile branch.

An axial cell cuts off laterally a supporting cell of similar size (though later the axial cell is usually larger), which in turn gives rise to the first three cells of the carpogonial branch. At this stage the supporting cell and carpogonial branch are together about 50 μ long. The third cell of the carpogonial branch cuts off a fourth, the carpogonium which develops the elongate trichogyne (Fig. 3a, b). The trichogyne projects through the whorled laterals of the thallus, reaching a length of up to 350 μ (Fig. 3c).

Several spermatia may adhere to one trichogyne, but only one develops a connection through the trichogyne wall. Very soon after fertilisation the trichogyne disintegrates, leaving the four-celled carpogonial branch.

On the upper side of the supporting cell a rounded auxiliary cell is cut off, and almost simultaneously the fertilised carpogonium divides transversely to form a small superior cell and larger inferior cell (Fig. 3d). From the lower part of the latter a small cell ("connecting cell") is cut off which enlarges and grows out towards the auxiliary cell. The auxiliary cell elongates to meet the connecting cell and ultimately fuses with it (Fig. 3e–g). The zygote nucleus presumably is left in the inferior cell when the carpogonium divides and transferred via the connecting cell to the auxiliary cell. The other cells of the old carpogonial branch commonly contain more than one nucleus at this stage. The first, and less frequently the second and third, cells of the carpogonial branch may cut off one

(rarely two) small cells which do not appear to have any function (Fig. 3e, f, h).

Comparatively few stages of actual fusion between carpogonium and auxiliary cell were found in comparison to large numbers of stages just before and shortly after, indicating that this transference of the diploid nucleus to the auxiliary cell is a rapid one.

The old carpogonial branch slowly disintegrates while the auxiliary (fusion) cell develops rapidly. Fusions between the auxiliary cell and other cells do not occur, but the auxiliary cell divides into a lower foot cell and upper central cell (Fig. 3h). The central cell buds off successive gonimolobes, each cutting off cells which divide to produce rounded groups of carpospores (Fig. 3i–l, Fig. 4). Only one fairly mature group of carpospores is present at any one time, with one or two younger groups developing. Mature carpospores average 75–80 μ wide by 100–120 μ long.

Two or three of the axial cells directly below those bearing carpogonial branches each bear a whorl of di- or trichotomously branched sterile filaments, which form a short, loose involucre around the carpospores (Fig. 4).

The mature carpospore groups are visible as small protrusions scattered irregularly over the thallus. The age of the carposporophytes shows a steady progression from the younger to the older parts of the thallus. On any one plant, however, there is not a very great difference between the oldest and youngest stages present.

SYSTEMATIC POSITION

As indicated in the introduction, *Gulsonia annulata* has been variously classified in the Cryptonemiales, Nemalionales, and Ceramiaceae by different authors. Previous accounts of the genus were all limited by inadequate material for study.

This investigation shows that *Gulsonia* is closely allied to *Crouania*, and belongs in the tribe Crouanieae of the Ceramiaceae. The
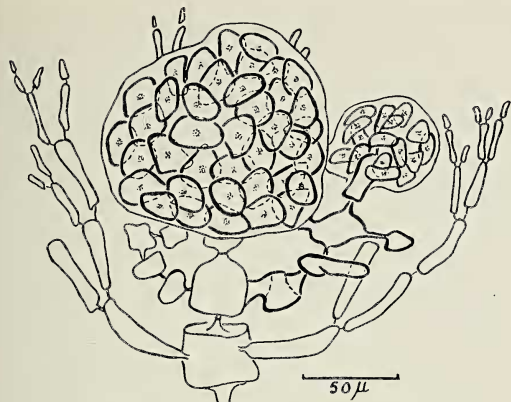
100 µ
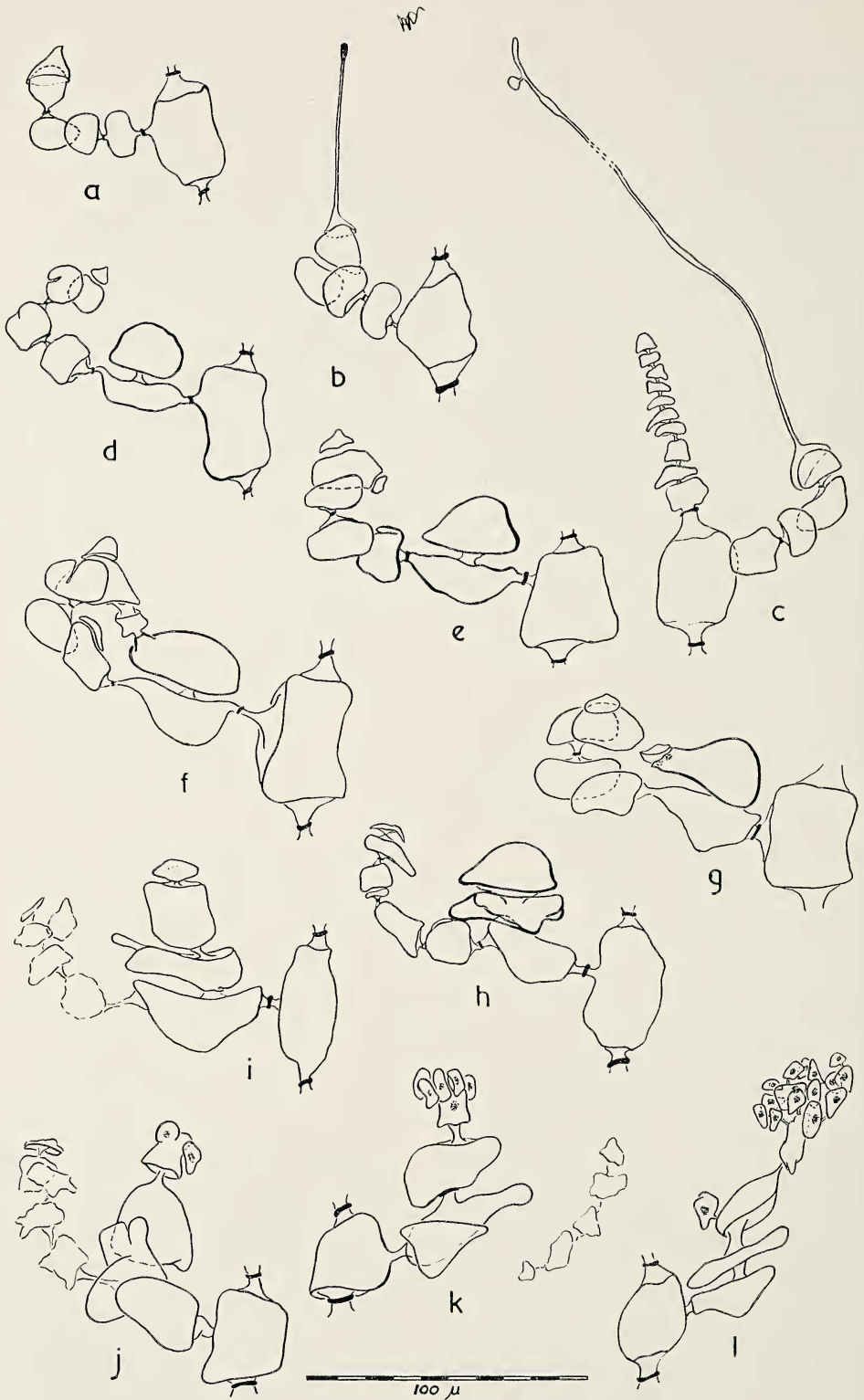
FIG. 4. Three stages in carpospore development. Sterile filaments from the axial cell immediately below the fertile axial cell form a loose involucre around the carpospore mass.

thallus construction, method of reproduction, and arrangement of the carpogonial branches are typical of the group. However, *Gulsonia* does differ from *Crouania* in two important features:

1. The carpogonial branches are borne on special fertile branches, whereas they are borne on the main axis in *Crouania*.

2. Lateral branches of unlimited growth are formed from the basal cell of a lateral whorl branch of limited growth, whereas in *Crouania* they develop directly from cells of the main axis.

These differences clearly indicate that *Gulsonia* is generically distinct from *Crouania*.

In 1940 J. and G. Feldmann separated *Crouania annulata* Berthold (a Mediterranean species) as a new genus *Crouaniopsis*, distinguished from *Crouania* by the same two features as distinguish *Gulsonia*. This separation, and J. and G. Feldmann's account of *Crouaniopsis* (see also Feldmann–Mazoyer, 1940) indicate that *Crouaniopsis* is generically identical with *Gulsonia* as has been recognised by Kylin (1956). In describing *Crouaniopsis*, Feldmann–Mazoyer (1940: 279) compares it with *Gulsonia*, noting the vegetative similarity of the two genera, but follows the description given by J. G. Agardh (1894) of the reproduction of *Gulsonia* and assumes the two to be generically as well as specifically distinct. Agardh's description is quite inadequate to indicate whether or not the two are generically distinct. The main features of *Gulsonia* (including *Crouaniopsis*) may be summarised as follows:

1. Thallus of uniaxial construction with short branches of limited growth in whorls of four from the upper part of each cell of the central axis, giving a noded appearance.

2. The development of young lateral branches of unlimited growth from the basal cells of the whorled laterals.

3. Four-celled carpogonial branches produced on special lateral branches which cease further development.

4. A short, loose involucre of filaments produced from axial cells at the base of the carposporophyte.

5. A loose cortication of the lower parts of the plant by filaments produced from the basal cells of the whorled laterals.

Gulsonia annulata Harvey and *Crouaniopsis annulata* (Berthold) J. and G. Feldmann are remarkably similar in form and appearance, but (judged from Feldmann–Mazoyer's figures and description) differ as follows:

FIG. 3. *Gulsonia annulata*. Stages in the development of the carposporophyte: a, Young four-celled carpogonial branch and supporting cell borne on axial cell of a fertile branch; b, trichogyne developing from the fourth (carpogonial) cell of the carpogonial branch; c, fusion of spermatia with fully developed trichogyne; d, stage after fertilization. Carpogonial cell divided and auxiliary cell cut off from upper face of the supporting cell; e, small connecting cell cut off from inferior carpogonial cell and elongation of auxiliary cell towards it; f, connecting cell fused with auxiliary cell while still attached to the inferior carpogonial cell; g, further fusion of connecting cell with auxiliary cell now completely separated from carpogonial cell; h, fusion cell (old auxiliary cell plus connecting cell) divided transversely to give an inferior foot cell and a superior central cell; i, first gonimolobe developed from central cell; j, first divisions in carpospore development from gonimolobe; k, further development of carpospores from gonimolobe; l, a second gonimolobe bud developing from central cell, while first bud continues further carpospore development.

1. The ultimate cells of the whorled laterals in *Crouaniopsis* are more elongate than in *Gulsonia annulata*.

2. *Gulsonia annulata* forms "gland" cells; *Crouaniopsis* apparently does not.

3. Tetrasporangia of *Gulsonia annulata* are formed on cells of the third order of the whorled laterals; in *Crouaniopsis* on cells of the second order.

4. In *Crouaniopsis* the spermatangia have an apical nucleus (Feldmann–Mazoyer 1940: 166), while in *Gulsonia annulata* the nucleus is median.

Direct comparison with preserved material of *Crouaniopsis* may show other differences, but they are clearly specifically distinct. Owing to the identity of the specific names, Kylin (1956) renamed the later species of Berthold. The genus *Gulsonia* thus comprises two species:

Gulsonia Harvey 1855

Gulsonia annulata Harvey (1855 : 334; 1860: 320, pl. 193A; 1863 : synop. 614). J. G. Agardh (1876 : 88; 1894 : 122, pl. II, f. 13; 1897 : 56). Kuetzing (1866 : pl. 66 c – e). De Toni (1897 : 66; 1924 : 151). Schmitz (1889: 435–456). Schmitz and Hauptfleisch (1897 : 329 – 331). Womersley (1948 : 161; 1950 : 178). Feldmann–Mazoyer (1940 : 279). Kylin (1956: 373).

DISTRIBUTION: Eucla, Western Australia to Georgetown, Tasmania.

Gulsonia mediterranea Kylin (1956: 373).
SYNONYMY: *Crouania annulata* Berthold (1882:518); *Crouaniopsis annulata* (Berthold) J. and G. Feldmann (1940: 181).
DISTRIBUTION: Western Mediterranean.

REFERENCES

AGARDH, J. G. 1876. *Species, Genera, et Ordines Algarum III* (1).
—— 1894. Analecta algologica, Cont. I. *Acta Univ. Lund* 29 : 1 – 144, pl. 2.
—— 1897. Analecta algologica, Cont. IV. *Acta Reg. Soc. Physiog. Lund* 8 : 1 – 106.
BERTHOLD, G. 1882. Ueber die Vertheilung der Algen im Golf von Neapel, nebst einem Verzeichniss der bisher daselbst beobachteten Arten. *Zool. Stat. zu Neapel, Mitt.* 3 : 393 – 536.
FELDMANN, J., and G. FELDMANN. 1940. *Crouaniopsis*, nouveau genre de Céramiacée Méditerranéenne. *Comptes Rend. des Seances de l' Académie des Sci.* 210:181 – 183.
FELDMANN – MAZOYER, G. 1940. *Recherches sur les Céramiacées de la Méditerranée Occidentale*. Algiers.
FRITSCH, F. E. 1945. *The Structure and Reproduction of the Algae*. Vol. II.
HARVEY, W. H. 1855. Short characters of some new genera and species of algae discovered on the coast of the colony of Victoria, Australia. *Ann. and Mag. Nat. Hist.* 15:332 – 336.
—— 1860. Algae. IN J.D. Hooker, *The Botany of the Antarctic Voyage*, Part III. *Flora Tasmaniae* 2: 282 – 343.
—— 1863. *Phycologia Australica* Vol. 5, synop. 614.
KUTZING, F. T. 1866. *Tabulae Phycologicae* Vol. 16.
KYLIN, H. 1956. *Die Gattungen der Rhodophyceen*. Lund.
SCHMITZ, F. 1889. Systematische Uebersicht der bisher bekannten Gattungen der Florideen. *Flora* 72:435 – 456.
SCHMITZ, F., and P. HAUPTFLEISCH. 1897. Rhodophyceae. IN Engler and Prantl, *Die Naturlichen Pflanzenfamilien* 1:327 – 335.
DE TONI, G. B. 1897. *Sylloge Algarum omnium hucusque Cognitarium*. Vol. 4.
—— 1924. *Sylloge Algarum omnium hucusque Cognitarium*. Vol. 6.
WOMERSLEY, H. B. S. 1948. The marine algae of Kangaroo Island II. The Pennington Bay region. *Roy. Soc. So. Austral., Trans.* 72(1):143 – 166.
—— 1950. The marine algae of Kangaroo Island III. List of species I. *Roy. Soc. So. Austral., Trans.* 73 (2):137 – 197.